

Arizona State University  
Center for Environmental Studies

Final Report

**“Mistletoe Abundance as a Bioindicator of Riparian Plant Stress”**

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December 1994

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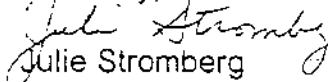
Tice Supplee  
Heritage IIPAM Project Coordinator  
Arizona Game and Fish Department  
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Dear Tice;

Enclosed please find a copy of the final report for the IIPAM Heritage grant entitled  
"Mistletoe Abundance as a Bioindicator of Riparian Plant Stress" (ASU grant  
BTT1296)

Thank you.

Sincerely,

  
Julie Stromberg  
Asst. Research Prof.

## Mistletoe Abundance as a Bioindicator of Riparian Plant Stress

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December, 1994

### Executive Summary

- \* This study tested the feasibility of using mistletoe abundance as a bioindicator of stress within two riparian vegetation types- velvet mesquite (*Prosopis velutina*) forests and Fremont cottonwood (*Populus fremontii*)-Goodding willow (*Salix gooddingii*) forests. Although mistletoe density did vary among habitats, the magnitude of the difference between stressed and unstressed habitats was too low to allow it to be useful as a sensitive bioindicator.
- \* Within mesquite forests, mistletoe (*Phoradendron californicum*) densities were slightly greater at sites classified as being more stressful (i.e., sites with lower groundwater tables). This may be due to increased mistletoe survivorship in the open tree canopies found at stressful sites, or to increased susceptibility to parasitism on stressed trees.
- \* The opposite trend was expressed within Fremont cottonwood-Goodding willow forests, where mistletoe (*P. tomentosum* subsp. *macrophyllum*) densities were greater at sites with the least stress (i.e., perennial vs. ephemeral stream sites). This pattern may result from increased abundance of mistletoe-feeding and dispersing birds within the high-density forests that develop along perennial rivers.
- \* Within high-density cottonwood stands, mistletoe density showed a trend of being highest at sites where cottonwood trees were well represented within larger size classes. Given that mistletoe density increased sharply with tree size (and thus age), the persistence of old, heavily infected trees may increase the rate at which mistletoe colonizes new generations of young cottonwoods.
- \* Among the host species, mistletoe densities were substantially higher on Fremont cottonwood than on Goodding willow or velvet mesquite.
- \* Mistletoe densities differed more between regions within the state (central vs. southern Arizona) than between sites of differing stress level within a region. Mistletoe densities were very low in the southern Arizona grassland region. Insufficient rainfall during the spring germination period may be a cause, which warrants further study.
- \* Differences in mistletoe abundance with respect to region, tree species, stand density, and age structure, have important implications for the abundance of bird species that utilize mistletoe berries as a food source.

Table 1. Location of cottonwood-willow study sites.

Stream	Flow pattern	Elevation (m)	Region
Santa Maria	Perennial	365	Central AZ desert
Hassayampa River	Perennial	597	Central AZ desert
Hassayampa River	Ephemeral	598	Central AZ desert
Date Creek	Perennial	878	Central AZ desert
Date Creek	Ephemeral	879	Central AZ desert
Verde River	Perennial	1015	Central AZ grassland
Agua Fria	Ephemeral	1140	Central AZ grassland
Santa Cruz River	Perennial	1000	Southern AZ grassland
Santa Cruz River	Ephemeral	930	Southern AZ grassland
Santa Cruz River	Perennial	1085	Southern AZ grassland
Santa Cruz River	Ephemeral	1110	Southern AZ grassland
Sonoita Creek	Perennial	1164	Southern AZ grassland
San Pedro River	Perennial	1180	Southern AZ grassland

### Methods and Study Areas

The basic study design involved surveying for mistletoe abundance within paired stream reaches, each differing in relative stress level. Cottonwood-willow stands were selected along reaches that differed in having perennial vs. ephemeral flow (Table 1). (Data remains to be collected along some ephemeral reaches, as well as along additional river pairs, to expand beyond the findings of this report). Mesquite stands were surveyed for mistletoe density along reach pairs that differ in depth to groundwater (Table 2). In some cases, the difference in depth to groundwater was due partly to differences in rates of groundwater pumpage (e.g., Tanque Verde), while in others a difference was assumed to exist due to position within the floodplain (e.g., high terrace vs. low terrace). Study areas were located within the Sonoran Desert and semidesert grassland regions of central and southern Arizona.

Table 2. Location of velvet mesquite study sites.

River site	Elevation (m)	Relative depth to groundwater	Region
Santa Maria	365	Shallow	Central AZ desert
Santa Maria	370	Deep	Central AZ desert
Hassayampa River	597	Shallow	Central AZ desert
Hassayampa River	600	Deep	Central AZ desert
Date Creek	875	Shallow	Central AZ desert
Date Creek	880	Deep	Central AZ desert
Tanque Verde Creek	805	Shallow	Southern AZ desert
Tanque Verde Creek	800	Deep	Southern AZ desert
Santa Cruz River	1000	Shallow	Southern AZ grassland
Santa Cruz River	930	Deep	Southern AZ grassland
Santa Cruz River	1085	Shallow	Southern AZ grassland
Santa Cruz River	1110	Deep	Southern AZ grassland
Sonoita Creek	1164	Shallow	Southern AZ grassland
Sonoita Creek	1167	Deep	Southern AZ grassland

Surveys were made by counting numbers of live and dead mistletoe plants on the Fremont cottonwood, Goodding willows, and velvet mesquite trees, using binoculars for the taller trees. Counts were made by two individuals, and the average of the two scores was reported. Surveys were conducted during the winter of 1993/94, when trees were dormant. For mesquite, two subsets of 20-25 trees were surveyed per site, except at Tanque Verde where four subsets of 25 trees were surveyed per site. Sample size for cottonwood and willow trees was three to four subsets of 20-25 trees each, depending on the extent of variation in tree size. Data also were collected on the trunk diameter of each surveyed tree (dbh, or diameter at breast height for cottonwood and willow, and bd, or basal diameter for mesquite), and on density, diameter and basal area of the cottonwood-willow stands (using the quadrat method).

Two measures of mistletoe abundance were calculated: density (mean density of mistletoe plants per tree) and frequency (percentage of trees with at least one mistletoe plant). At sites with a wide range of tree sizes, regression analysis was used to determine whether mistletoe density varied significantly with tree size (dbh or bd).

Differences in mistletoe density between cottonwood and willow trees within sites were analyzed with one-way analysis of covariance, with tree size as the covariate. Differences between sites in mistletoe density and frequency were analyzed with two-way analysis of variance (ANOVA), using data for paired sites only. Factors included in the ANOVA were water availability (ephemeral vs. perennial for cottonwood, or deep vs. shallow groundwater for mesquite) and region within the state. An additional ANOVA was performed on the cottonwood data, using the two factors of region and cottonwood-willow basal area (subjectively divided into sites with average basal area of  $<10 \text{ m}^2/\text{ha}$  or  $>10 \text{ m}^2/\text{ha}$ ). For the cottonwood ANOVAs, the dependent variable in the ANOVA was mistletoe density on trees within the 41-60 cm dbh range, to standardize for effects due to tree size. Mistletoe density for the mesquite ANOVA represents densities averaged across all trees, because mean mesquite trunk diameter did not differ substantially between sites.

## Results

### Cottonwood-willow stands

*Variation within populations.* With the exception of one site (Agua Fria), the density of mistletoe (*Phoradendron tomentosum* subsp. *macrophyllum*) increased significantly with tree size (dbh) at all sites where mistletoe was abundant ( $P < 0.01$ , regression analysis). The relationship between mistletoe density and tree size typically was linear (Table 3). Small trees (i.e., those with dbh  $< 10$  cm) generally had no mistletoe, while the largest cottonwood trees (100-200 cm dbh) in some cases had over 100 mistletoe plants (Fig. 1).

Table 3. Linear regression equations relating mistletoe (*Phoradendron tomentosum* subsp. *macrophyllum*) density to tree trunk diameter (dbh, in cm), for selected study sites.

	Equation	$r^2$	Sig. level
Fremont cottonwood at Hassayampa River	$y = -9.8 + 0.46x$	0.49	$<0.001$
Fremont cottonwood at Date Creek	$y = -12.8 + 1.07x$	0.67	$<0.001$
Goodding willow at Hassayampa River	$y = -0.2 + 0.02x$	0.07	0.002
Goodding willow at Date Creek	$y = 1.3 + 0.17x$	0.10	0.024

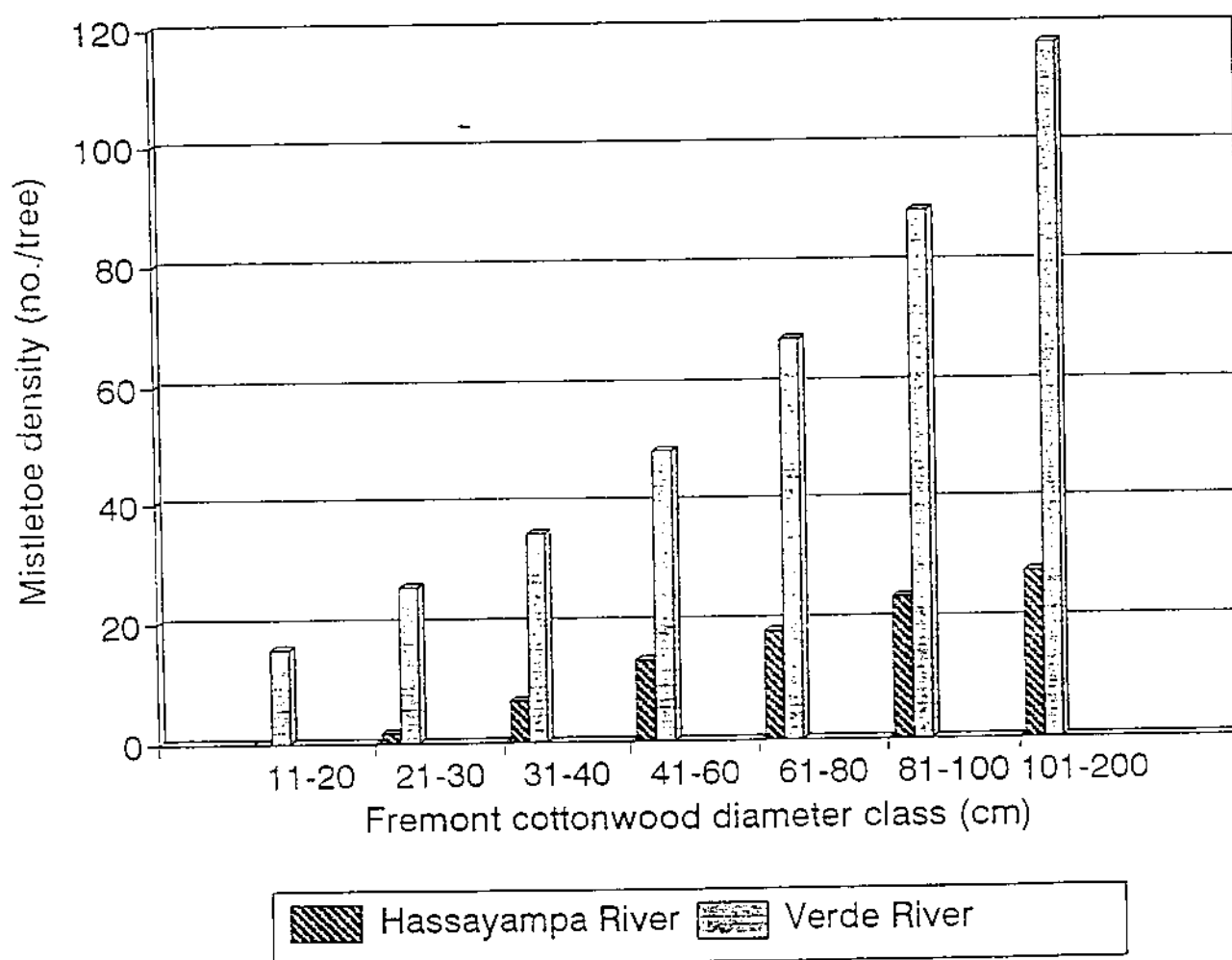


Figure 1. Mean mistletoe density in relation to cottonwood tree size, for two selected perennial river study sites.



Table 4. Abundance of mistletoe (*Phoradendron tomentosum* subsp. *macrophyllum*) on Fremont cottonwood and Goodding willow trees. Data are for trees within the 41-60 cm dbh size class.

Stream site	Flow pattern	Fremont cottonwood		Goodding willow	
		Frequency (%)	Density (plants/tree)	Frequency (%)	Density (plants/tree)
Santa Maria	P	43	1±2	0	0±0
Hassayampa River	P	94	14±12	19	1±1
Hassayampa River	E	40	8±10	25	1±1
Date Creek	P	100	37±15	100	20±11
Date Creek	E	100	30±18	100	15±14
Verde River	P	83	49±6	29	2±7
Agua Fria	E	100	7±4	Size class not present	
Santa Cruz River	P	0	0±0	0	0±0
Santa Cruz River	E	0	0±0	Size class not present	
Santa Cruz River	P	38	2±2	0	0±0
Santa Cruz River	E	0	0±0	Size class not present	
San Pedro River	P	0	0±0	0	0±0
Sonoita Creek	P	5	<1±<1	0	0±0

*Variation between species.* At all sites, Fremont cottonwood supported significantly higher densities of mistletoe than did Goodding willow, when controlling for size ( $P < 0.01$ , analysis of covariance, with dbh as covariate). For example, Fremont cottonwood trees within the 41-60 cm dbh class along the Verde River supported an average of 48 mistletoe plants, compared to less than 3 on Goodding willow trees of similar size (Fig. 2; Table 4). Additionally, because of its tendency to be more well represented in larger size classes in comparison to Goodding willow, Fremont cottonwood contributed disproportionately to the mistletoe population within the cottonwood-willow stands.

*Variation among sites.* The factor contributing most significantly to differences among sites in mistletoe density (Table 5) and frequency (data not shown) was region within the state. Few cottonwood or willow trees at sites in the southern Arizona grassland region (Santa Cruz River, Sonoita Creek, San Pedro Rivers) had any mistletoe, and densities per tree were low. Cottonwoods and willows in the central desert and grassland, however, generally supported abundant mistletoe populations.

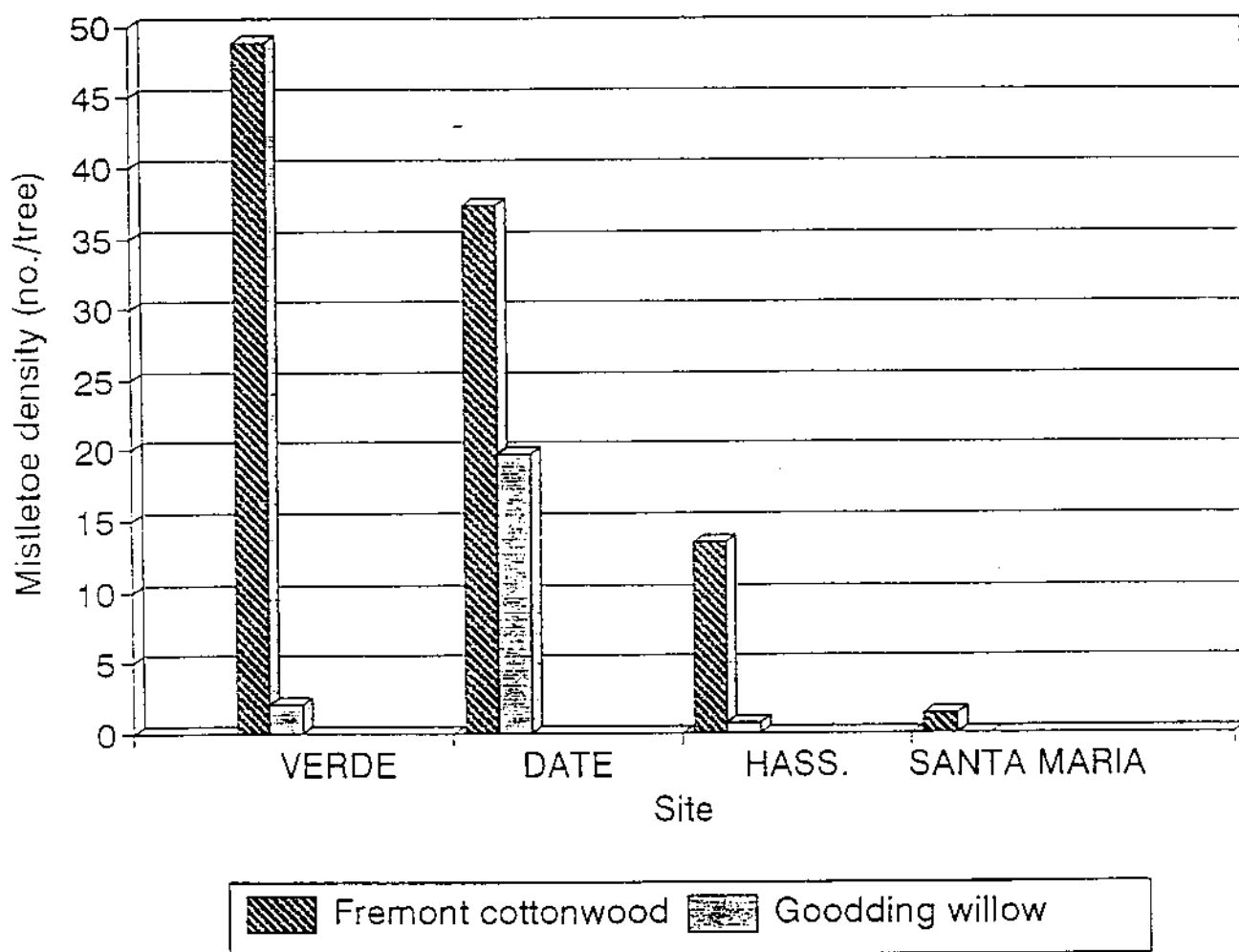


Figure 2. Mean density of mistletoe (*Phoradendron tomentosum* subsp. *macrophyllum*) on mature Fremont cottonwood and Goodding willow trees (41-60 cm dbh), at four study sites in central Arizona (Verde River, Date Creek, Hassayampa River, and Santa Maria River).

Table 5. Results of analysis of variance, comparing mistletoe density on Fremont cottonwood trees between sites differing in region within Arizona, and in flow status or basal area.

Source of variation	Sum of squares	Degrees of freedom	Mean square	F	Sig. of F
Main effects	1568	2	784	4.8	0.056
Region	1344	1	1344	8.3	0.028
Perennial vs. ephemeral flow	224	1	224	1.4	0.284
2-way interactions	180	1	180	1.1	0.332
Explained	1849	3	616	3.8	0.077
Residual	972	6	162		
Total	2822	9	313		
Main effects	1450	2	725	6.7	0.029
Region	869	1	869	8.1	0.029
Cottonwood-willow basal area	386	1	386	3.6	0.106
2-way interactions	329	1	329	3.1	0.130
Explained	2178	3	726	6.7	0.024
Residual	643	6	107		
Total	2822	9	313		

After region, the factor most strongly related to mistletoe density was cottonwood-willow basal area ( $P = 0.11$ , Table 5). This effect was a positive one, with mistletoe densities being greater at sites with higher basal area ( $>10 \text{ m}^2/\text{ha}$ ) than with lower basal area ( $<10 \text{ m}^2/\text{ha}$ ). Effects due to the presence of perennial vs. ephemeral flow were not significant ( $P = 0.284$ ), although there was an observable trend for mistletoe densities to be greater at perennial sites than at the paired ephemeral site (Table 4). Although not statistically analyzed, it also was observed that mistletoe densities were greatest at sites with high stand basal area and an abundance of large, old trees. For example, among the perennial river sites in central Arizona, mistletoe densities were greater at the Verde River and Date Creek than at the Hassayampa and Santa Maria Rivers, all of which support high density cottonwood stands (Fig. 2). Both of the former stands had an abundance of large, old trees (i.e., those greater than about 80 cm dbh), while the latter are dominated by relatively young trees (i.e., those less than about 30-40 years, unpub. data of author).

## Mesquite stands

*Variation within populations.* The scale-leaved *P. californicum* was the only species of mistletoe observed on the velvet mesquite trees. Although mistletoe density varied with tree size, the relationship was not as strong as for cottonwoods, perhaps because the range of variation in tree size was fairly limited in most of the mesquite stands. At Tanque Verde Creek, where trees ranged in size from <10 cm to >60 cm basal diameter, mistletoe increased significantly as trunk diameter increased ( $r^2 = 0.10$ ,  $P < 0.001$ , for shallow groundwater sites;  $r^2 = 0.13$ ,  $P < 0.001$  for deeper groundwater sites) (Fig. 3).

*Variation between species.* Although the species of mistletoe observed on mesquite differed from that on cottonwoods and willows, between-species comparisons can still be made. Densities of *P. californicum* in the mesquite stands generally were somewhat lower than were densities of *Phoradendron tomentosum* subsp. *macrophyllum* in the adjacent cottonwood stands, on a per-tree basis. At Hassayampa River (perennial section), for example, mesquite trees (30 cm mean basal diameter) averaged <1 mistletoe per tree, compared to about 5 for similar sized cottonwoods; respective values for adjacent mesquite and cottonwood stands at Date Creek were about 2 and 8. Overall, mean mistletoe densities per mesquite tree (site averages) ranged from 0 to 4 for trees averaging about 30 cm dbh, compared to 0 to 30 for cottonwoods in the same size range.

Table 6. Results of analyses of variance, comparing mistletoe density and frequency on velvet mesquite trees, between sites differing in region and relative depth to groundwater.

Source of variation	Mistletoe density				Mistletoe frequency			
	df	Mean square	F	Sig. of F	Mean square	F	Sig. of F	
Main effects	2	6.433	5.693	0.029	2760	5.122	0.037	
Region	1	9.013	7.976	0.022	4602	8.540	0.019	
Deep vs. shallow gw	1	3.853	3.410	0.102	918	1.705	0.228	
2-way interactions	1	3.000	2.655	0.142	630	1.170	0.311	
Explained	3	5.289	4.680	0.036	2050	3.805	0.058	
Residual	8	1.130			538			
Total	11	2.264			951			

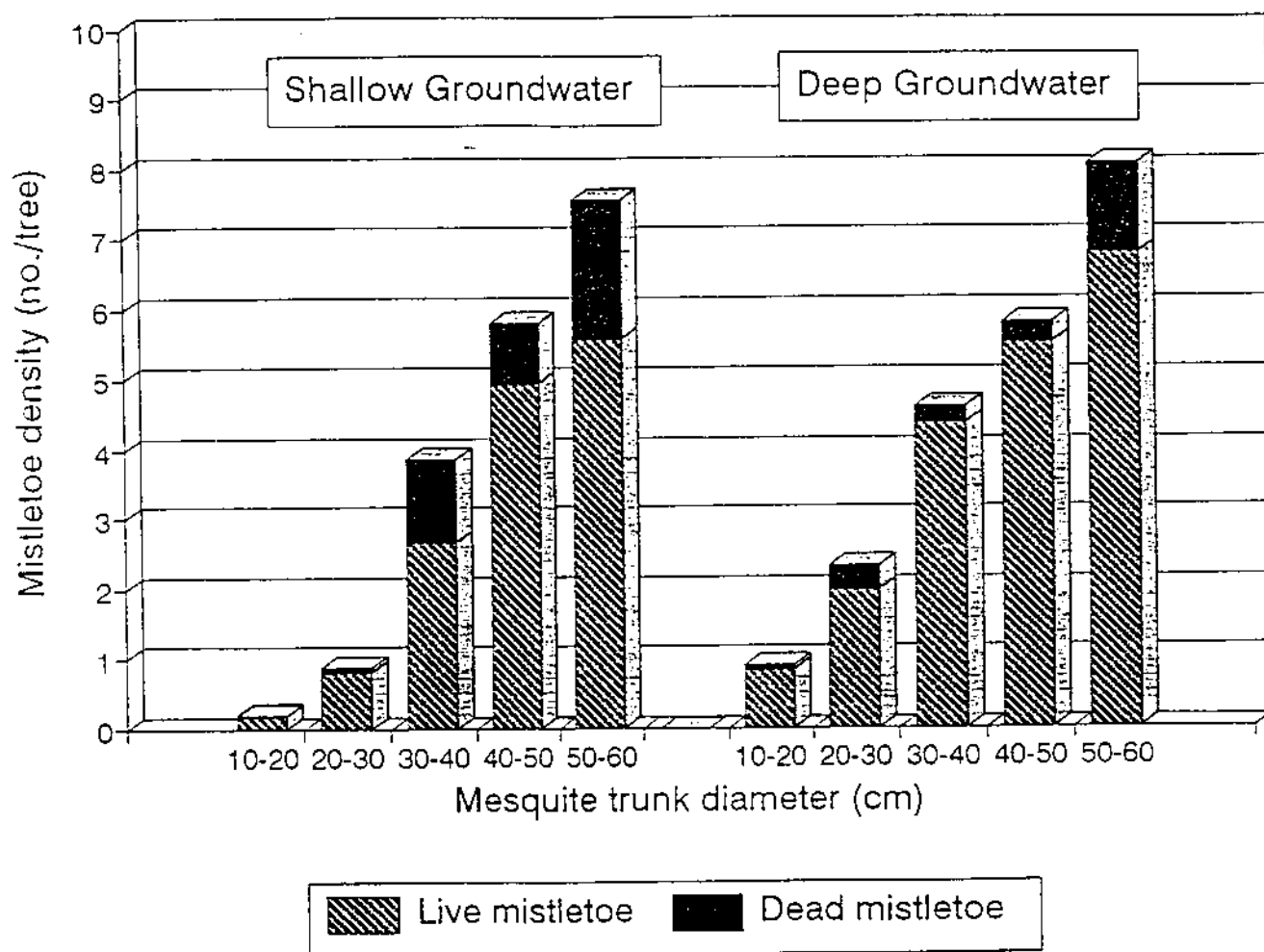


Figure 3. Abundance of live and dead mistletoe (*P. californicum*) on velvet mesquite trees at Tanque Verde Creek, in relation to tree size and groundwater depth.

*Variation among sites.* Region within the state was the variable most significantly related to differences in mistletoe abundance among sites (Table 6). No mistletoe were present on mesquite trees at most sites in the southern Arizona grassland region, whereas from 4 to 85% of the trees within the central Arizona desert sites supported mistletoe (Table 7). Mistletoe densities and frequencies also were high within the southern Arizona desert sites (Tanque Verde sites), which were excluded from the analysis of variance.

Table 7. Abundance of mistletoe (*P. californicum*) at velvet mesquite study sites.

River site (cm)	Relative stress level	Mesquite basal diameter (%)	Mistletoe density (plants/tree)			Mistletoe frequency
			Live	Dead	Total	
Santa Maria	Low	27±6	0.0±0.0	0.1±0.2	0.1±0.2	5
Santa Maria	High	30±6	2.8±4.4	0.1±0.2	2.9±4.5	60
Hassayampa River	Low	29±11	0.1±0.3	No data	0.1±0.3	4
Hassayampa River	High	32±7	1.1±2.9	No data	1.1±2.9	25
Date Creek	Low	30±7	1.8±2.2	0.2±0.5	2.0±2.5	65
Date Creek	High	29±7	3.7±4.4	0.9±1.8	4.6±5.0	85
Tanque Verde Ck	Low	35±9	2.5±3.4	0.8±1.2	3.3±4.6	49
Tanque Verde Ck	High	35±11	3.3±4.0	0.4±1.1	3.7±4.1	55
Santa Cruz River	Low	35±6	0.0±0.0	0.0±0.0	0.0±0.0	0
Santa Cruz River	High	35±9	0.4±1.0	0.0±0.0	0.4±1.0	9
Santa Cruz River	Low	32±8	0.0±0.0	0.0±0.0	0.0±0.0	0
Santa Cruz River	High	38±11	0.0±0.0	0.0±0.0	0.0±0.0	0
Sonoita Creek	Low	36±11	0.0±0.0	0.0±0.0	0.0±0.0	0
Sonoita Creek	High	35±12	0.0±0.0	0.0±0.0	0.0±0.0	0

In addition to effects due to region, there also was a trend for mistletoe density to vary with relative depth to groundwater ( $P = 0.102$ ). The pattern, however, was opposite that for the cottonwood-willow stands in that mistletoe density was slightly greater, rather than lower, in the stands with reduced water availability. Although the magnitude of the difference was not great, there was a consistent trend for mesquite at deep groundwater sites to support about one or two more mistletoe plants than those at the paired shallow groundwater site. At Tanque Verde Creek, trees growing in the less stressful areas showed a tendency to have greater relative abundances of dead mistletoes in comparison to trees at the deeper groundwater sites, although this pattern was not consistent across other sites.

## Discussion

*Utility as bioindicator.* This study indicates that mistletoe density does vary to some extent as a function of habitat stress, but the magnitude of difference is not great between paired stressed and unstressed sites. Thus, it is not a sensitive bioindicator of stress for either Fremont cottonwood-Goodding willow forests or velvet mesquite forests. Lack of sensitivity is due, in part, to the overriding influence of other factors that influence mistletoe abundance.

*Regional differences in mistletoe abundance.* Region within the state was the variable most significantly related to mistletoe density on all three tree species examined. Low abundance of *P. californicum* and *P. tomentosum* subsp. *macrophyllum* within the southern Arizona grassland region may be a result of a variety of factors. First, Loranthaceae is a tropical family and many of its members are sensitive to frost. Thus, hard freezes at the high elevations of southern Arizona may contribute to low mistletoe abundance. However, the presence of abundant mistletoe at sites of similarly high elevation in central Arizona suggests that frost is probably not the main factor at play.

A second possible factor is regional variation in amount and timing of winter and spring rainfall, if these rains are important for mistletoe germination and seedling survival. Although there is lack of specific information on germination requirements of the two species of concern, Bray (1910) indicates that the seeds ripen in winter, about a year after fertilization, and germinate in spring in response to rainfall and temperature increase. If seeds have short viability and must germinate soon after maturation, low rainfall during the spring warm season in southern Arizona could play a role in reducing mistletoe germination and survival. For example, using a mean monthly temperature of 60 F as a purely speculative value for a germination temperature optimum, data from Sellers and Hill (1974) indicates that this temperature at the southern Arizona study sites is attained during a month with little rain (e.g. rainfall in April at Tumacacori, along the Santa Cruz River, averages 0.23 inch). In central Arizona, in contrast, at low and high elevations, rain is abundant during the month when temperatures average 60 F (e.g., Alamo Station, near the Santa Maria River, 0.66 inches in March; and at Montezuma Castle, near the Verde River study site, 0.78 inches in April). At the one southern Arizona site where mistletoe were abundant (Tanque Verde), rain was abundant (0.74 inches) in the month (March) when temperatures averaged 60 F.

Variation in abundance of mistletoe-feeding birds is a third factor that may influence regional patterns of mistletoe abundance. It is a well established fact that mistletoe seeds are adapted for dispersal by birds. The seeds of nearly all mistletoes are covered with an adhesive mucilaginous tissue, viscin, which is of importance in bird-mediated dispersal and in the attachment of the seeds to the host surface

(Gedalovich et al. 1988). Both of the mistletoe species studied rely on bird species such as phainopepias (see *Ecological functions*) to disperse mistletoe seeds between trees, although wind and rain can result in localized (mainly within-tree) seed dispersal. Regional patterns of abundance of mistletoe-feeding birds were examined by looking at summaries of annual Christmas bird counts (published in American Birds). These data indicate that at least one such species was present in relatively high numbers in all study regions, thereby suggesting that birds probably are not a primary factor limiting the abundance of mistletoe in the southern Arizona grassland zone.

*Stress-related changes in mistletoe abundance.* Within the mesquite study areas, there was a trend for mistletoe densities to be slightly elevated at sites considered to be under stress due to the presence of naturally deep water tables and/or human-related groundwater decline. This pattern is consistent with that reported by Judd et al. (1971), who describe an increase in mistletoe densities on water-stressed mesquite trees along the dewatered Gila River, prior to death of the trees. One physiological basis for this increase is the reduced ability of stressed plants to fight infection by parasites or pathogenic organisms (Kozlowski et al. 1991). Another is reduced mortality of mistletoe from light-limitation (Bray 1910), as the tree canopies become more open due to water stress (Stromberg, Tress et al. 1992). This pattern of increasing mistletoe density may become more pronounced over time as stress becomes intense or prolonged, due to positive feedback interactions between bird populations and mistletoe populations.

Relationships between habitat stress and mistletoe density within cottonwood-willow stands were opposite of that for mesquite. These findings are similar to those reported by Gregg and Ehleringer (1991), who found greater abundance of *P. juniperum* on juniper trees that had less negative water potentials and access to greater amounts of water. Again, several factors may be responsible. First, low water stress in the host plant may increase rates of mistletoe seedling survivorship. Second, high mistletoe densities may be a consequence of the high tree densities that are supported by perennial streams with shallow, stable water tables. High tree densities, in turn, may provide better habitat for birds that disperse mistletoe seeds. Additionally, because mistletoe produced unisexual, wind-pollinated flowers, males and females need to be in relatively close proximity for fertilization. Thus, there may be greater probability of fertilization success in high density stands.

Within the cottonwood-willow stands, there also was a trend for higher mistletoe densities at sites with an abundance of large, old trees. This pattern is consistent with other studies that show mistletoe to have an aggregated dispersion pattern (Elias 1988), with infection rate expanding from discrete loci such as large trees. Infection rate of young trees has been reported to increase with proximity to large trees (Geils and Mathiasen 1990), and seedlings growing under a heavily infested overstory have higher infection rates (Mathiasen 1986). Survivorship of old, heavily infected



cottonwood trees may play a major role in providing a seed source for mistletoe recolonization of young cottonwoods, particularly given the high rate of population turnover that can occur in frequently flooded riparian habitats. At sites with frequent intense flooding, post-flood buildup of mistletoe populations may occur slowly in the absence of abundant recolonization sources. The same may be true if the plant community has low resistance to flood damage, if for example, poor landuse practices have reduced riparian plant cover and increased flood-related tree loss. In riparian zones located along streams that drain small watersheds and flood infrequently, or in riparian zones with a high level of resistance to flood damage, the persistence of old, infected trees would serve to maintain high levels of mistletoe over time.

*Host species differences in mistletoe abundance.* Reasons for the higher densities and frequencies of *P. tomentosum* subsp. *macrophyllum* on Fremont cottonwood vs. Goodding willow are unknown. It is known that trees within a species can vary in resistance to mistletoe infestation, due in part to variable production of flavonoids and other secondary defense chemicals (Hariri et al. 1991). A similar mechanism may explain between-species difference in infection susceptibility.

*Ecological functions and importance of mistletoe.* Mistletoe has many functions within ecosystems. Some species of mistletoe can kill trees, while others are only infrequently associated with tree mortality (Reid and Lange 1988). Various species of mistletoe also can reduce canopy cover, increase branch mortality, cause growth decline, decrease seed production, and induce malformation of stems (Singh and Carew 1989; Baker et al. 1992; Reid et al. 1992). As a consequence, infected trees commonly are cleared from conifer forests to salvage merchantable timber. During this study, tree death due to heavy infestation of mistletoe was observed at only one site, Date Creek, which was the site with the greatest density of willow-supported mistletoe and the second highest density of cottonwood-supported mistletoe. At this site, several heavily infested young willow trees and old cottonwood trees were observed to be either dead or to have substantial branch mortality.

Mistletoe also can cause changes in stand transpiration rates. Mistletoe commonly has a higher transpiration rate and lower water use efficiency than its host plant, in part because a high transpiration rate is essential to allow for nitrogen accumulation (Whittington and Sinclair 1988; Davidson and Pate 1992). This can cause high stand transpiration rates, particularly in winter due to mistletoe's evergreen nature. However, mistletoe infection also can exacerbate host plant water stress and cause greater stomatal closure, which can counterbalance transpirational losses from the mistletoe itself (Bernhofer and Gay 1989). Mistletoe also can cause infected trees to have lower leaf water potentials and lower leaf nitrogen contents than uninfected trees (Ehleringer et al. 1986).

Mistletoe berries have high nutritional quality, and serve as a valuable source of food for birds and other animals including white-tailed deer (Gallina 1988). The fruits of *P.*

*californicum* and *P. tomentosum* subsp. *macrophyllum* ripen in winter, and many species of birds are dependent on the berries as a winter food source. Phainopeplas, for example, feed almost exclusively on mistletoe berries as they move through the lower Colorado River Valley in fall and winter and spring, and undergo population declines and reproductive failure in years when the mistletoe berry crop is small due to frost (Waisberg 1975; Anderson and Ohmart 1978). Spatial distribution of the phainopeplas is seasonally correlated with high mistletoe abundance (Anderson and Ohmart 1978). Northern mockingbirds and sage thrashers also have been observed to maintain territories around mistletoe clumps. Phainopeplas and black-tailed gnatcatcher sometimes build nests in mistletoe clumps. Other frugivorous birds that feed heavily or occasionally on mistletoe berries include cedar waxwing, American robin, western and mountain bluebirds, house finch, Gambel's quail, Gila woodpecker, northern flicker, and Townsend's solitaire (Rosenberg et al. 1991).

Destruction of riparian habitat is an issue of concern for bird species as well as other animals. Clearing of mistletoe-infected mesquite woodlands from the Colorado River floodplain, for example, has been implicated as a cause of local rarity of the western bluebird in the Yuma area (Rosenberg et al. 1991). The spatial variation in mistletoe abundance documented in this study highlights the unique functional role of each riparian zone, and the need to maintain a network of healthy riparian sites. Overall, sites with highest mistletoe infection, and thus arguably the greatest value to mistletoe-feeding birds, were those located in central Arizona that had high cottonwood-willow basal area (a condition allowed by perennial flow and low water stress) and an abundance of large trees (a condition allowed by watershed management practices that increase rates of rainfall absorption and reduce the intensity of peak flows). Given the importance of mistletoe as a wildlife resource, further studies which track long-term trends in mistletoe abundance and expand upon other aspects of its distribution or ecology should be undertaken. Data collected for this study will provide a foundation upon which additional studies can expand.

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